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# Seasonal succession of phytoplankton species on the coast of A Coruña (Galicia, northwest Spain)

*B. Casas, M. Varela and A. Bode*

Centro Ocranográfico de A Coruña. Instituto Español de Oceanografía. Apdo. 130. 15080 A Coruña, Spain

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**ABSTRACT**

Phytoplankton species composition was monitored monthly at two stations on the continental shelf off A Coruña (Galicia, northwest Spain). The deeper station (80 m) was sampled between May 1989 and December 1992. The coastal station (20 m) was studied during 1992. In each sampling, water samples were taken from selected depths throughout the water column. Microflagellates formed the bulk of phytoplankton, being dominant all year long, followed by diatoms, which dominated during phytoplankton blooms. The samples studied were arranged into five groups, according to environmental conditions defined for the main oceanographic periods in the area. Each group showed a characteristic phytoplankton species composition. The most important phytoplankton blooms occurred during spring and autumn. However, major phytoplankton abundances were also detected during upwelling events in the summer. Several species of the genus *Chaetoceros,* especially *C. socialis* (Lauder, 1864) were dominant during blooms, and accompanying species, e.g. *Lauderia borealis* (Gran, 1900), were important during spring and autumn. *Leptocylindrus danicus* (Cleve, 1889) made a major contribution to phytoplankton abundance during summer upwelling events. In contrast with studies conducted in neighbouring areas, dinoflagellates never dominated during summer stratification periods, probably because of the very frequent upwelling events, which caused destabilisation of the water column. During winter mixing and in deeper waters, we found a mixed community comprising species that are present throughout the year, but in very low densities, as well as resuspended diatoms from sediment. In 1992, at the coastal station, red-tide events occurred, and some species of dinoflagellates (e.g. *Gymnodinium catenatum* Graham, 1943) reached densities of well over 100 cells $ml^{-1}$. Considering the entire series of observations, the most noteworthy features are a decrease in the magnitude of diatom blooms during the study period and, on the contrary, an increase in the abundance of microflagellates.

**Key words:** Phytoplankton, succession, seasonality, diatoms, dinoflagellates, microflagellates, northwest Spain.

***RESUMEN***

***Sucesión estacional de fitoplancton en la costa de A Coruña (Galicia, noroeste de España)***

*Se estudia la composición de especies y grupos taxonómicos de fitoplancton con una frecuencia aproximadamente mensual en dos estaciones de la plataforma continental frente a A Coruña (Galicia, noroeste de España). La estación más profunda (80 m) fue muestreada entre mayo de 1989 y diciembre de 1992. La estación costera (20 m) fue estudiada durante 1992. En cada muestreo se recogieron muestras repartidas por toda la columna de agua. El grupo de fitoplancton más numeroso fue el de los microflagelados, siempre dominantes en todas las épocas del año, seguido de las diatomeas, responsables de las principales proliferaciones de fitoplancton registradas. Las observaciones se clasificaron en cinco grupos según las características ambientales definidas para los principales periodos oceanográficos de esta zona. Cada uno de estos grupos presentó una composición de especies de fitoplancton característica. Las mayores proliferaciones de fitoplanc-*

*ton se produjeron en primavera y otoño, pero también se registraron elevadas abundancias durante episodios de afloramiento en verano. Varias especies del género* Chaetoceros, *especialmente* C. socialis *(Lauder, 1864), fueron las principales responsables de estas proliferaciones, acompañadas de otras especies de diatomeas como* Lauderia borealis *(Gran, 1900) en primavera y otoño, y* Leptocylindrus danicus *(Cleve, 1889) en el afloramiento de verano. A diferencia de lo encontrado en otras zonas próximas, los dinoflagelados no llegan a hacerse dominantes en el periodo de estratificación térmica de verano, probablemente debido a la frecuencia de los episodios de afloramiento. Durante el periodo de mezcla invernal y en las capas profundas de la columna de agua se encuentra una mezcla de especies presentes todo el año, aunque con bajas abundancias, y también diatomeas del sedimento resuspendidas. En 1992, especialmente en la estación costera, se produjeron episodios de marea roja durante el verano, superando algunas especies de dinoflagelados (como* Gymnodinium catenatum *Graham, 1943) 100 células ml$^{-1}$. Considerando toda la serie de observaciones, se aprecia una disminución en la magnitud de las proliferaciones de diatomeas y un incremento en la abundancia de microflagelados en los últimos años.*

***Palabras clave:*** *Fitoplancton, sucesión, estacionalidad, diatomeas, dinoflagelados, microflagelados, noroeste de España.*

## INTRODUCTION

Phytoplankton species succession is linked to changes in the stratification of water-column surface layers (Harris, 1986). Morphological and physiological adaptations of phytoplankton cells enable some groups of species to compete advantageously during the various steps of the continuous transition between vertical mixing and stratification of the surface layer (Margalef, 1978; Smayda, 1980). In temperate waters, one of the main causes for stratification is the steady surface heating during spring and summer due to increasing solar irradiance (Walsh, 1988).

In general, the succession progresses in several steps, from initial phases where strong vertical mixing favours the dominance of chain-forming diatoms, to mature phases where water column stratification favours the strategy of dinoflagellates and other flagellates that can swim to zones rich in light or nutrients (Margalef, 1978). However, in areas affected by episodic upwelling events, the upwelling of cold waters to surface layers of the water column radically changes the seasonal pattern of stratification, keeping the phytoplankton communities of these areas in the initial stages of succession (Estrada and Blasco, 1985).

On the Galician coast (northwest Spain), which is affected by upwelling events essentially between March and October (Fraga, 1981), seasonal variation of phytoplankton species composition has been well studied in the rias, specially the Rias Bajas (Margalef, Duran and Saiz, 1955; Durán *et al.,* 1956; Nunes *et al.,* 1984; Figueiras and Niell, 1987b; Figueiras and Ríos, 1993), but also in the Rias Altas (Campos and Mariño, 1984; Mariño *et al.,* 1985). Other studies have described phytoplankton species composition in the rias during certain seasons (Margalef, 1956; Campos and Mariño, 1982; Varela, 1982; Blanco, 1985; Figueiras and Niell, 1987a; Figueiras and Pazos, 1991a,b). However, references to phytoplankton on the Galician continental shelf off the rias are quite scarce. The only data available previously were for certain months (Estrada, 1984; Varela *et al.,* 1987a,b), but no studies had been conducted on phytoplankton succession in the area. For studies of annual phytoplankton succession on the continental shelf of the Bay of Biscay, see Estrada (1982) and Fernández and Bode, Casas and Varela (1994).

The scope of the present study is to describe the seasonal variability of phytoplankton abundance and characteristic species of the main oceanographic periods described for La Coruña's continental shelf (Bode, Casas and Varela, 1994; Casas *et al.,* 1997).

## MATERIALS AND METHODS

Samples of water and phytoplankton were taken at two stations off A Coruña (figure 1), at approximately monthly intervals. Station 2 (depth of 80 m) was sampled from May 1989 to December 1992. Station 4 (depth of 20 m) was sampled from January to December 1992. In each sampling, temperature, salinity, irradiance, dissolved nutrients, chlorophyll, and particulate nitrogen and carbon were measured. Methods used to determine these parameters and detailed information on these data

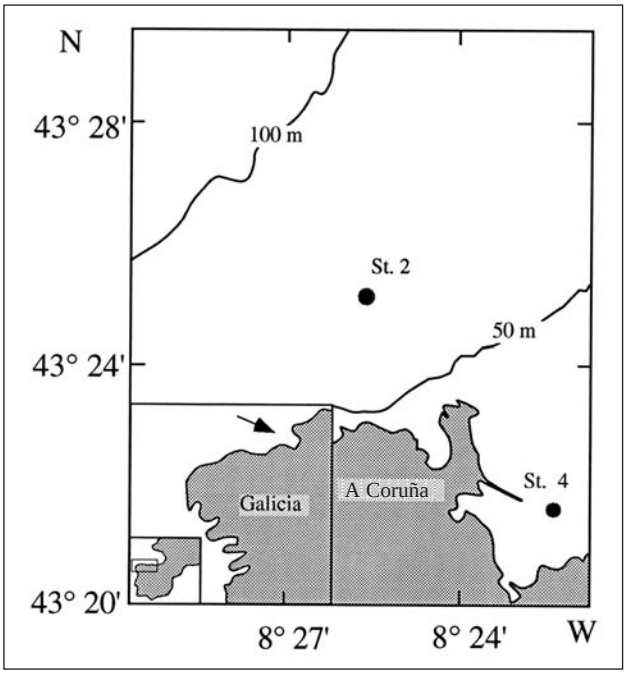


Figure 1. Location of study area and sampled stations

can be found in Casas (1995) and Casas *et al.* (1997). Phytoplankton samples were taken with Niskin bottles at standard depths of 0, 5, 10, 20, 30, 40 and 70 m from station 2, between May 1989 and December 1991. From 1992 on, sampling depths were chosen according to *in situ* irradiance profiles, so that samples were taken at 100, 50, 25, 10 and 1% of surface irradiance levels (Casas, 1995).

Phytoplankton samples were preserved with Lugol's solution and kept in darkness until counting, using Utermöhl's technique (1958). Observation of samples was carried out using a Nikon Diaphot inverted microscope with Nomarsky phase-contrast system. Magnification powers of ×100, ×200 and ×400 were used, according to the size of organisms. Results are expressed in cells $ml^{-1}$.

When the organisms were too small (usually smaller than 30 µm) to be classified at the genus or species level, they were included in wider groups, e.g. flagellates, dinoflagellates, and so on. Flagellates, which can belong to different taxonomic categories, were divided into three size classes: 2-5 µm, 5-10 µm and larger than 10 µm. The diatom relative abundance index was calculated by dividing the total number of diatoms by the total number of diatoms plus dinoflagellates for each sample.

To define the groups of characteristic species for each oceanographic situation, a discriminant analysis was carried out using the species found during the period 1989-1992 at station 2 and during 1992 at station 4. The groups of samples defined *a priori* were those described by Casas (1995) and Casas *et al.* (1997), using the hydrographic properties of the water column, along with the nutrient and chlorophyll concentrations observed in each case. The analysis was carried out with 387 samples and 49 species or taxa, selecting those taxa whose relative frequency was higher than 20 %, to avoid the effect of rare species. Data were logarithmically transformed. The Mulva 4 (Wildi and Orloci, 1990) statistical package was used in the analysis.

## RESULTS

### Temporal distribution of cellular abundance

Distribution of total abundance of diatoms and dinoflagellates in station 2 (figure 2a) shows that higher abundances occur over short periods of time during autumn (> 7 000 cells $ml^{-1}$ in 1989), summer (up to 6 000 cells $ml^{-1}$ in 1990) and spring (around 2 000 cells $ml^{-1}$ in 1989 and 1990). These periods coincide with maximum values in chlorophyll and particulate material concentrations at these stations (Casas, 1995; Casas *et al.,* 1997). The relative abundance of diatoms was usually high (index values higher than 0.5) throughout the period of study, with diatoms becoming even more dominant during the aforesaid blooms. The relative abundance of diatoms was low during winter and some periods of summer (figure 2b), essentially due to a decrease in diatom abundance in the former case, and to the relative increase of dinoflagellates in the latter. Even though the distribution pattern of diatom relative abundance is similar among different years and also at both stations, values of diatom abundance higher than 1 000 cells $ml^{-1}$ were observed more often in 1989 and 1990 than in the other years.

Microflagellates always constituted the bulk of phytoplankton. Microflagellates of 2-5 µm, counted in the samples since 1991, showed abundances well over 10 000 cells $ml^{-1}$ in some autumn and summer samples (figure 3a). The abundance of microflagellates measuring 5-10 µm does not show a clear seasonal pattern of dominance, at least until 1991, when abundances higher than 1 000 cells $ml^{-1}$ were recorded in surface layers during late

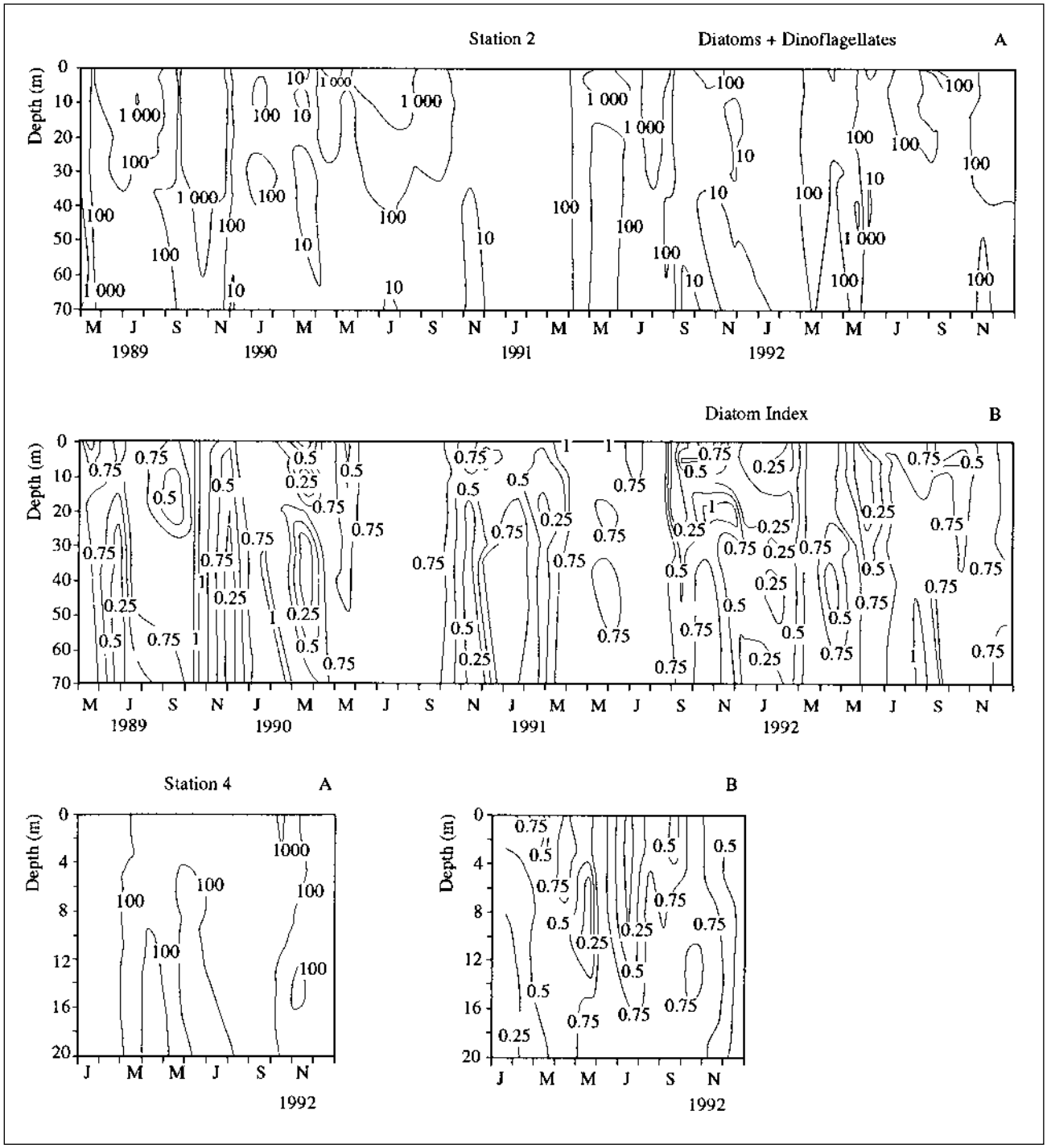


Figure 2. Temporal variation of total abundance of diatoms plus dinoflagellates (cells ml$^{-1}$, A) and relative abundance of diatoms index (%, B)

summer, extending the layer of higher abundance to steadily increasing depths throughout 1992 (figure 3b). Variations in abundance of this size fraction of flagellates at station 4 were relatively small (always around 1 000 cells ml$^{-1}$). Larger microflagellates (> 10 μm) were especially dominant during summer periods, even though they showed abundances higher than 100 cells ml$^{-1}$ in autumn and winter during 1992 (figure 3c). Taking into account all fractions, but especially the mid-size fraction (5-10 μm), an increase in microflagellate abundance was observed during 1992.

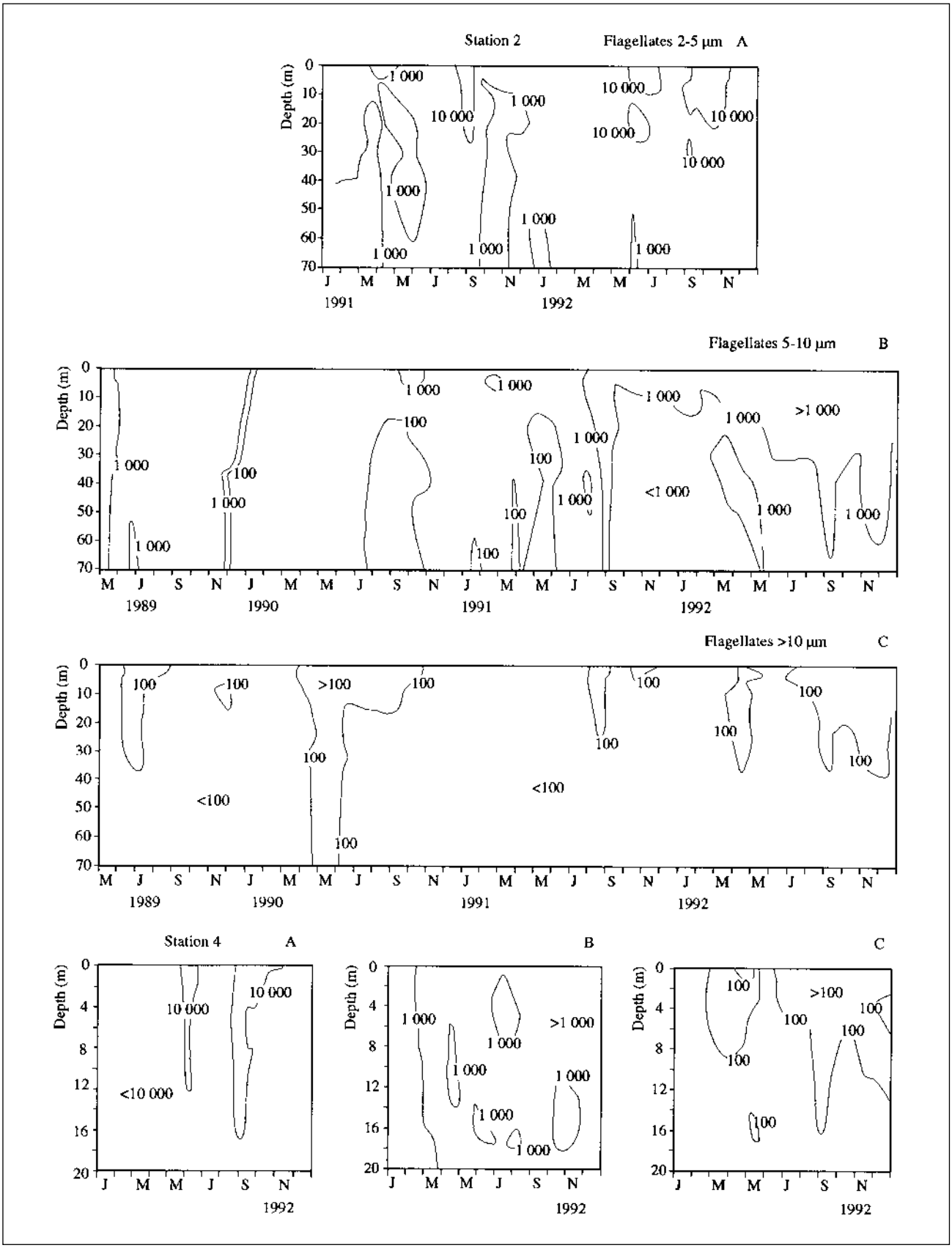


Figure 3. Temporal variation of abundance of microflagellates, 2-5 µm (A), 5-10 µm (B) and larger than 10 µm (C), expressed in cells ml$^{-1}$

**Succession of species assemblages**

During the present study, 205 species or categories of phytoplankton were recognised. A complete list can be found in Casas (1995). To summarise the information obtained, a discriminant analysis was conducted on the most abundant species (table I). Samples were classified into five groups according to characteristics of environmental variables in selected oceanographic stages, summarised in table II, as defined in Casas (1995) and Casas *et al.* (1997). Group 1 contains samples representative of phytoplankton blooms during spring and autumn, when chlorophyll concentrations were higher than 1 mg $m^{-3}$ and a slight density gradient was present in the upper layer of the water column. Group 2 includes samples from the thermal stratification situation observed during

Table I. Mean values (cells $ml^{-1}$), standard error of mean (s.e.m.) and presence (n) of the 49 taxa used in the discriminant analysis. The code used in figure 4 is indicated

| Code | Species or group | n | Mean | s.e.m. |
|---|---|---|---|---|
| DIN < 30 | Dinoflagellates < 30 µm | 357 | 16.32 | 1.54 |
| DIN > 30 | Dinoflagellates > 30 µm | 73 | 0.55 | 0.18 |
| DINACU | *Dinophysis acuminata* | 34 | 0.19 | 0.17 |
| GYRSPI | *Gyrodinium spirale* | 83 | 0.33 | 0.09 |
| GYRGLA | *Gyrodinium glaucum* | 74 | 0.35 | 0.13 |
| MASSPP | *Massartia* spp. | 98 | 2.33 | 0.74 |
| MICSPP | *Micracanthodinium* spp. | 35 | 0.20 | 0.14 |
| PROMIC | *Prorocentrum micans* | 44 | 0.64 | 0.72 |
| PROBIP | *Protoperidinium bipes* | 42 | 0.22 | 0.15 |
| PRODIA | *Protoperidinium diabolus* | 24 | 0.11 | 0.11 |
| SCRTRO | *Scrippsiella trochoidea* | 87 | 2.93 | 1.98 |
| ASTJAP | *Asterionella japonica* | 29 | 1.89 | 2.42 |
| BACDEL | *Bacteriastrum delicatulum* | 30 | 2.01 | 2.19 |
| CERBER | *Cerataulina bergoni* | 66 | 0.34 | 0.13 |
| CHFCHW | *Chaetoceros affinis* (+ var. *willei*) | 85 | 7.07 | 4.70 |
| CHACUR | *Chaetoceros curvisetus* | 15 | 0.62 | 1.38 |
| CHADID | *Chaetoceros didymus* | 70 | 2.96 | 2.74 |
| CHASOC | *Chaetoceros socialis* | 119 | 83.74 | 33.41 |
| CHASPP | *Chaetoceros* spp. | 101 | 6.69 | 4.61 |
| CENTR | Centric diatoms | 57 | 0.30 | 0.16 |
| PENN | Pennate diatoms | 81 | 0.43 | 0.13 |
| LAUBOR | *Lauderia borealis* | 54 | 4.31 | 2.77 |
| LEPDAN | *Leptocylindrus danicus* | 124 | 26.83 | 23.87 |
| LEPMIN | *Leptocylindrus minimus* | 83 | 3.82 | 1.84 |
| NAVSAL | *Navicula cf. salinarum* | 73 | 0.18 | 0.06 |
| NAVSPP | *Navicula* spp. | 37 | 0.28 | 0.21 |
| NITEPI | *Nitzschia* spp. | 55 | 1.15 | 0.59 |
| NITLON | *Nitzschia longissima* | 266 | 4.50 | 0.64 |
| PARSUL | *Paralia sulcata* | 39 | 0.49 | 0.37 |
| PSEDEL | *Pseudonitzschia delicatissima* | 129 | 2.34 | 0.72 |
| PSEPUN | *Pseudonitzschia pungens* | 212 | 21.76 | 8.14 |
| RHIDEL | *Rhizosolenia delicatula* | 154 | 10.57 | 3.15 |
| RHIFRA | *Rhizosolenia fragilissima* | 51 | 1.70 | 1.12 |
| RHISHU | *Rhizosolenia shrubsolei* | 64 | 0.47 | 0.25 |
| RHISET | *Rhizosolenia setigera* | 56 | 0.25 | 0.11 |
| RHISTO | *Rhizosolenia stolterforthii* | 71 | 1.46 | 0.67 |
| SCHDEL | *Schroederella delicatula* | 54 | 3.38 | 2.77 |
| SKECOS | *Skeletonema costatum* | 88 | 7.57 | 5.90 |
| THANIT | *Thalassionema nitzschioides* | 78 | 1.09 | 0.67 |
| THAFAL | *Thalassiosira fallax* | 72 | 2.69 | 1.60 |
| EUGL | Euglenaceae | 39 | 0.16 | 0.11 |
| DISSPE | *Distephanus speculum* | 72 | 0.32 | 0.12 |
| SOLSET | *Solenicola setigera* | 91 | 11.76 | 4.35 |
| COCO | Coccolithophorids | 43 | 1.67 | 1.59 |
| PHAPOU | *Phaeocystis poucheti* | 75 | 6.72 | 2.81 |
| CRYP | Cryptophyceae | 300 | 41.60 | 6.10 |
| MESRUB | *Mesodinium rubrum* | 87 | 0.46 | 0.20 |

Table II. Mean values, standard deviation (s.d.), number of samples (n), maximum value (max) and minimum (min) of temperature (t, °C), salinity (S, usp), concentrations of nitrite (µmol $l^{-1}$), nitrate (µmol $l^{-1}$), phosphate (µmol $l^{-1}$) and dissolved silicate (µmol $l^{-1}$), and chlorophyll-*a* in two size fractions: particles larger than 12 µm (Chl-*a* > 12 µm, mg $m^{-3}$) and smaller than 12 µm (Ch-*a* < 12 µm, mg $m^{-3}$), grouping the observations according to oceanographic periods defined by Casas (1995) and Casas *et al.* (1997) for the study area. Samples from winter period also include those obtained below the photic zone in other periods

| Period | | t | S | Nitrite | Nitrate | Phosphate | Silicate | Chl-*a* > 12 µm | Chl-*a* < 12 µm |
|---|---|---|---|---|---|---|---|---|---|
| Phytoplankton blooms | n | 38 | 38 | 64 | 60 | 64 | 33 | 64 | 64 |
| | mean | 13.21 | 35.69 | 0.40 | 2.30 | 0.42 | 0.62 | 1.98 | 0.72 |
| | s.d. | 0.84 | 0.30 | 0.24 | 2.07 | 0.28 | 0.55 | 2.24 | 0.71 |
| | max | 15.47 | 35.93 | 0.94 | 9.28 | 1.77 | 2.82 | 11.10 | 3.71 |
| | min | 12.27 | 34.38 | 0.10 | 0.10 | 0.11 | 0.12 | 0.10 | 0.10 |
| Stratification | n | 31 | 21 | 37 | 36 | 41 | 26 | 46 | 46 |
| | mean | 15.27 | 35.75 | 0.45 | 0.98 | 0.30 | 0.52 | 0.61 | 0.85 |
| | s.d. | 1.19 | 0.23 | 0.30 | 1.03 | 0.14 | 0.27 | 0.59 | 0.66 |
| | max | 17.86 | 36.68 | 0.90 | 4.60 | 0.70 | 1.20 | 3.24 | 2.85 |
| | min | 12.90 | 35.44 | 0.10 | 0.12 | 0.15 | 0.18 | 0.10 | 0.12 |
| Winter | n | 114 | 105 | 174 | 170 | 174 | 104 | 180 | 180 |
| | mean | 13.31 | 35.61 | 0.48 | 5.03 | 0.54 | 1.61 | 0.38 | 0.39 |
| | s.d. | 0.65 | 0.26 | 0.28 | 2.02 | 0.23 | 1.30 | 0.36 | 0.27 |
| | max | 14.90 | 36.20 | 1.55 | 14.31 | 1.55 | 5.38 | 3.29 | 1.76 |
| | min | 11.51 | 34.65 | 0.11 | 0.77 | 0.15 | 0.19 | 0.10 | 0.00 |
| Summer upwelling | n | 33 | 33 | 63 | 68 | 68 | 34 | 68 | 68 |
| | mean | 14.68 | 35.67 | 0.39 | 3.13 | 0.42 | 1.19 | 1.52 | 0.83 |
| | s.d. | 1.59 | 0.16 | 0.21 | 2.71 | 0.19 | 1.03 | 1.41 | 0.80 |
| | max | 17.50 | 36.23 | 0.85 | 9.84 | 0.87 | 3.47 | 6.71 | 3.94 |
| | min | 11.68 | 35.35 | 0.11 | 0.12 | 0.12 | 0.10 | 0.10 | 0.00 |
| Red tide and downwelling | n | 29 | 29 | 29 | 29 | 29 | 26 | 29 | 29 |
| | mean | 16.97 | 35.63 | 0.44 | 1.84 | 0.38 | 1.27 | 0.64 | 0.56 |
| | s.d. | 1.53 | 0.13 | 0.27 | 2.10 | 0.16 | 1.08 | 0.39 | 0.36 |
| | max | 18.98 | 35.88 | 0.96 | 7.29 | 0.74 | 4.90 | 1.68 | 1.90 |
| | min | 13.49 | 35.38 | 0.11 | 0.15 | 0.17 | 0.10 | 0.11 | 0.14 |

summer, when a sharp density gradient was evident in the water column, concentrations of dissolved nutrients were low, and chlorophyll concentration were usually lower than 1 mg $m^{-3}$. Winter samples and those corresponding to deep layers of water column during different periods were included in Group 3. In this group, samples are characterised by a well-mixed water column with relatively high nutrient concentrations and low values of chlorophyll, as well as low abundances of phytoplankton cells. Group 4 comprises samples from summer upwelling events, characterised by relatively cold water (around 13 °C) and rich in nutrients (i.e. > 5 µM of nitrate) near the surface. Samples from this group show chlorophyll concentrations higher than 1 mg $m^{-3}$, and a total phytoplankton abundance similar to that observed during spring blooms. Finally, Group 5 includes two types of rare episodes: red tides and downwelling. These two phenomena were observed during late summer of 1992, and both are related to the presence of warm and low- density surface waters. In the case of red tide, proliferations of dinoflagellates were observed, with abundances well over 100 cells $ml^{-1}$. In the case of downwelling, warm surface water was found at lower depths of the water column, coinciding with a change in the surface direction that accumulated surface water towards the coast (Casas *et al.*, 1997).

When plotting the species in relation to the first and second discriminant functions (figure 4) it can be observed that the first discriminant function (FD1) groups together, in its positive part, diatoms –including *Lauderia borealis* (Gran, 1900), *Thalassiosira fallax* (Meunier, 1910), *Chaetoceros socialis* (Lauder, 1864), *Chaetoceros curvisetus* (Cleve, 1899), *Schroederella delicatula* (Pavillard, 1913) and *Rhizosolenia delicatula* (Cleve, 1898)– that are all dominant species during spring and autumn blooms as well as upwelling events. The negative part of FD1 separates species typical of stratified

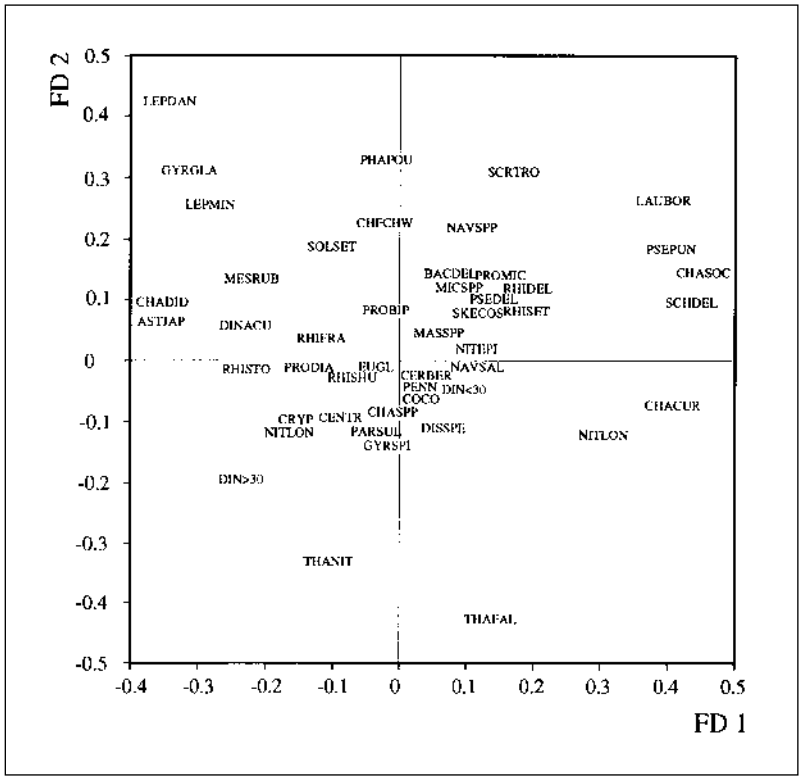


Figure 4. Projection of the phytoplankton species on the first two axes of discriminant analysis (FD1 and FD2). Codes for species are shown in table I

waters –including the dinoflagellates *Gyrodinium glaucum* (Kofoid and Swezy, 1921), *Protoperidinium diabolus* (Balech, 1974), *Protoperidinium bipes* (Balech, 1974)– and diatoms that dominate during phases of relaxing upwelling, e.g. *Rhizosolenia stolterfothii* (Peragallo, 1898), *Rhizolenia fragilissima* (Bergon, 1903), *Chaetoceros affinis* (Hustedt, 1930), *Leptocylindrus danicus* (Cleve, 1889) and *Leptocylindrus minimus* (Gran, 1915). The second discriminant function (FD2) shows, in its positive part, most of the dinoflagellate and diatom species, whereas in the negative portion appear those species typical of winter mixing and/or deep waters, e.g. *Navicula cf. Salinarum* (Grunow, 1878), *Paralia sulcata* (Cleve, 1873) and *Dictyocha speculum* (Ehrenberg, 1839).

The distribution of phytoplankton samples with regard to FD1 and FD2 presents a separation in the space among the five groups, separating the positive part of FD1 the samples corresponding to spring, autumn and most of upwelling blooms from summer stratification samples and those belonging to red tide and downwelling events in the negative part (figure 5). The second function (FD2) also separates in its positive part samples of spring, autumn and upwelling, but also, those of summer stratification, red tide and downwelling. The negative part of FD2 includes winter and deep-water samples. The discriminant analysis correctly grouped together more than 88 % of samples in the initial groups, which clearly confirms the descriptive utility of the identified oceanographic stages.

The species characterising Group 1 are essentially diatoms, among which *C. socialis*, *L. borealis*, *Rhizosolenia setigera* (Brightwell, 1858) and *S. delicatula*, which can top 1 000 cells ml$^{-1}$, are the most noteworthy species. *C. socialis* reached very high abundances (maximum of 6 000 cells ml$^{-1}$ in autumn 1989) during spring and autumn blooms at both stations (figure 6a). It also appeared in high abundances during upwelling events (> 2 000 cells ml$^{-1}$ in 1991, station 2). However, this species reached lower densities during 1992 than in previous years. Diatoms of the genus *Chaetoceros* were generally dominant in all observed blooms. The main difference between spring and autumn blooms with regard to upwelling blooms was in the number and type of associated species that appeared along with *Chaetoceros*. Some of these species occurred exclusively during spring and autumn, e.g. *L. borealis* (figure 6b). Others were more frequent during summer upwelling events, e.g. *L. danicus* (figure 7a). Also during summer upwelling

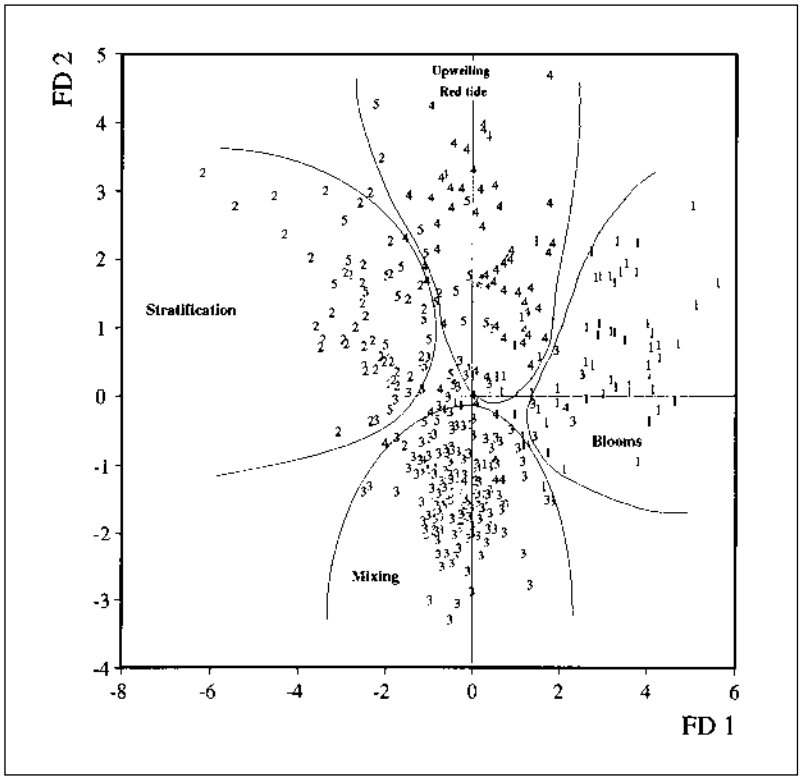


Figure 5. Projection of samples on the first two axes of the discriminant analysis (FD1 and FD2). The numbers indicate the group to which each sample was initially assigned and which corresponds to the oceanographic periods defined (see text): (1): phytoplankton blooms during spring and autumn; (2): summer thermal stratification; (3): winter mixing and deep samples; (4): summer upwelling; (5): red tides and downwelling of surface waters

(Group 4), *Leptocylindrus minimus, Pseudonitzschia delicatissima* (Heiden, 1928) and *C. affinis* (+ var. *willei)* showed abundances higher than 100 cells ml$^{-1}$. *Pseudonitzschia cf. pungens* (Hasle, 1993) and the Prymnesiophyceae *Phaeocystis poucheti* (Lagerheim, 1893) were also abundant during upwelling, but with lower densities. On the contrary, summer stratification phases (Group 2) were characterised by a mixture of diatoms and dinoflagellates, with somewhat lower abundances compared with those of blooms, and which can also appear in other periods. Among diatoms, *L. danicus* and some species of the genera *Chaetoceros* and *Massartia* were the most abundant during this period, but none exceeded 100 cells ml$^{-1}$. An illustrative example of a dominant dinoflagellate during this phase is *Gyrodinium spirale* (Kofoid and Swezy, 1921), which only once showed abundances higher than 10 cells ml$^{-1}$ (figure 7b).

The species appearing in the samples of Group 3 were usually present throughout the year. *Skeletonema costatum* (Cleve, 1873), for instance, showed relatively high abundances in January and February 1990, even though it also appeared during blooms in summer and autumn. Some other meroplanktonic diatoms, e.g. *Paralia sulcata*, were typical of these samples, and were present in deeper waters, not only during winter mixing, but also during other seasons, when resuspension of bottom material occurs (figure 8b).

Species causing red tides (Group 5) appeared with higher abundances at the inshore station. During July 1992, *Alexandrium lusitanicum* (Balech, 1985) (figure 9a) and *Prorocentrum micans* (Eherenberg, 1837) (figure 9b) were dominant, the latter observed throughout the spring and early summer, although never in high abundances. In September, *Gymnodinium catenatum* (Graham, 1943) (figure 9c) and *Scrippsiella trochoidea* (Loeblich III, 1976) (figure 9d) dominated the dinoflagellate population at the time when downwelling of warm surface waters occurred (Casas, 1995; Casas *et al.,* 1997).

## DISCUSSION

The values of phytoplankton abundance observed in the present study fall within the range of those previously described by other authors for Galician waters (Varela, 1982; Estrada, 1984; Varela *et al.,* 1987a,b; Valdés *et al.,* 1991; Varela, 1992), but they are higher than those cited for the Cantabrian Sea (Estrada, 1982; Fernández and Bode, 1994). The succession model is similar to that expected

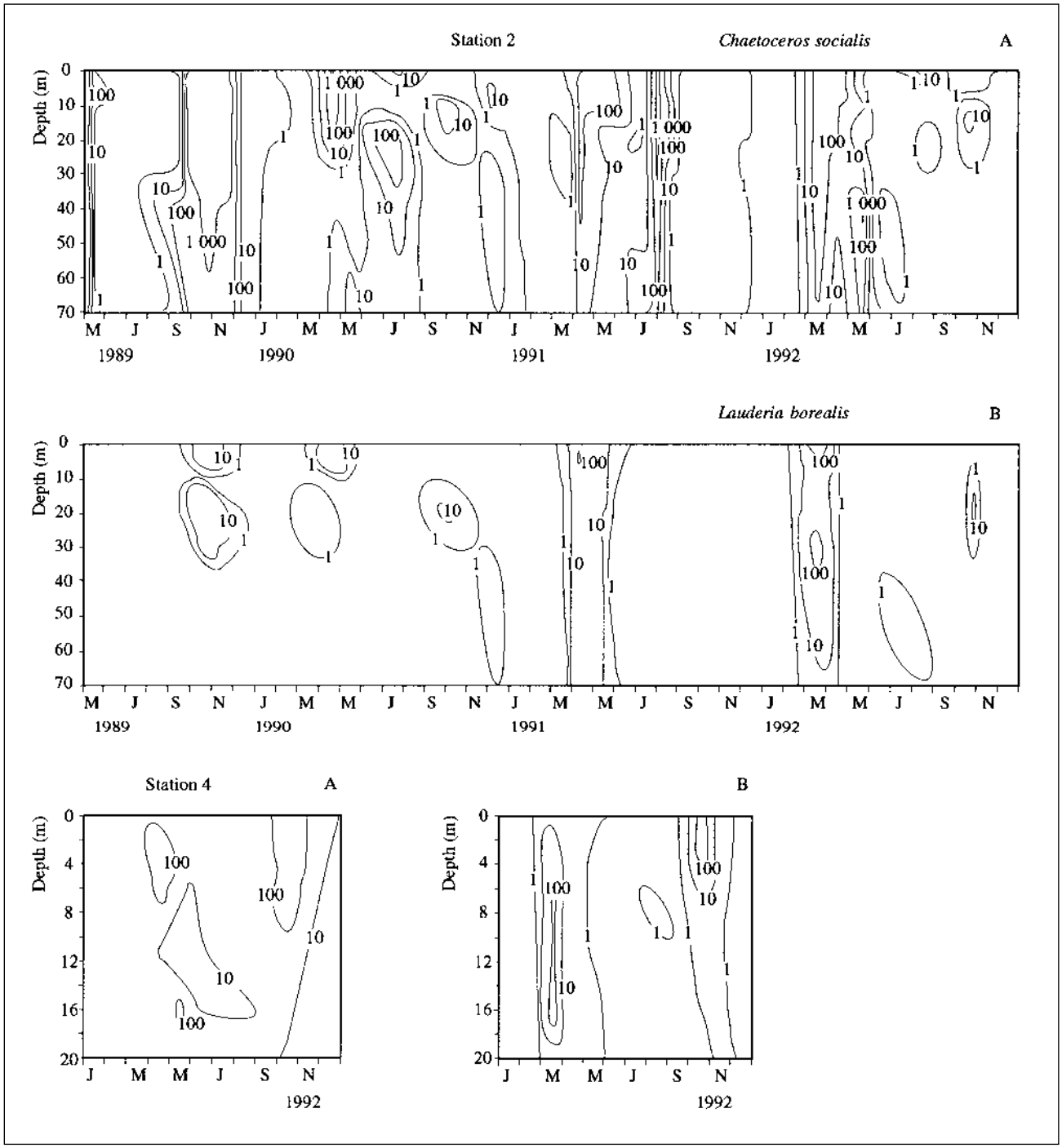


Figure 6. Distribution of abundance of some species characteristic of periods of phytoplankton proliferation, including summer upwelling: *Chaetoceros socialis* (A, cells ml$^{-1}$) and *Lauderia borealis* (B, cells ml$^{-1}$)

for this area of the northeast Atlantic, corresponding to a temperate zone (Margalef, 1978; Smayda, 1980; Harris, 1986). However, some differences were found with respect to the classical model of succession, these being mainly the dominance of microflagellates throughout the year, the frequent proliferations of diatoms, and the red tides.

Microflagellates were numerically the most important phytoplankton group throughout the study period and in all succession stages, representing more than 70 % of total phytoplankton during all periods. Their importance had previously been reported in both tropical waters (Hulburt, Ryther and Guillard, 1960; Takahashi and Bienfang, 1983) and

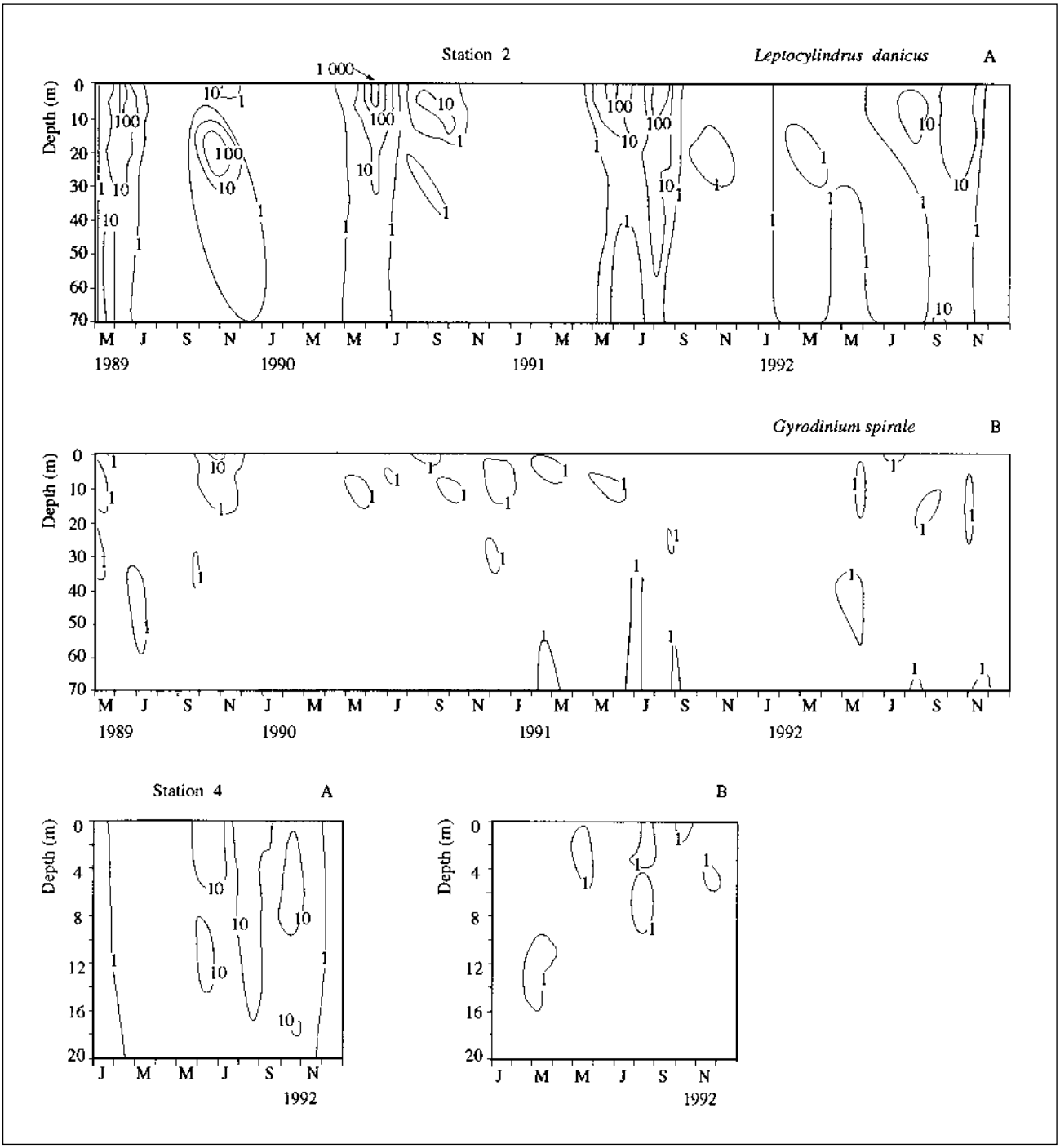


Figure 7. Distribution of abundance of some species dominant during the summer stratification period: *Leptocylindrus danicus* (A, cells ml$^{-1}$) and *Gyrodinium spirale* (B, cells ml$^{-1}$)

temperate waters (Malone, 1980). They constitute an important part of the phytoplankton community in Galician waters, as shown by the findings of Estrada (1984), Varela *et al.* (1987a,b) and Valdés *et al.* (1991), among other authors. Generally, these organisms predominate in waters with low nutrient concentrations, because their high surface/volume ratio enables them to advantageously utilise light and nutrients during summer stratification and downwelling periods. Sometimes they appear in large numbers accompanying or following diatom proliferations (Nielsen and Richardson, 1989), as in the present study. However, it is known that many of these flagellates are auxotrophs or heterotrophs

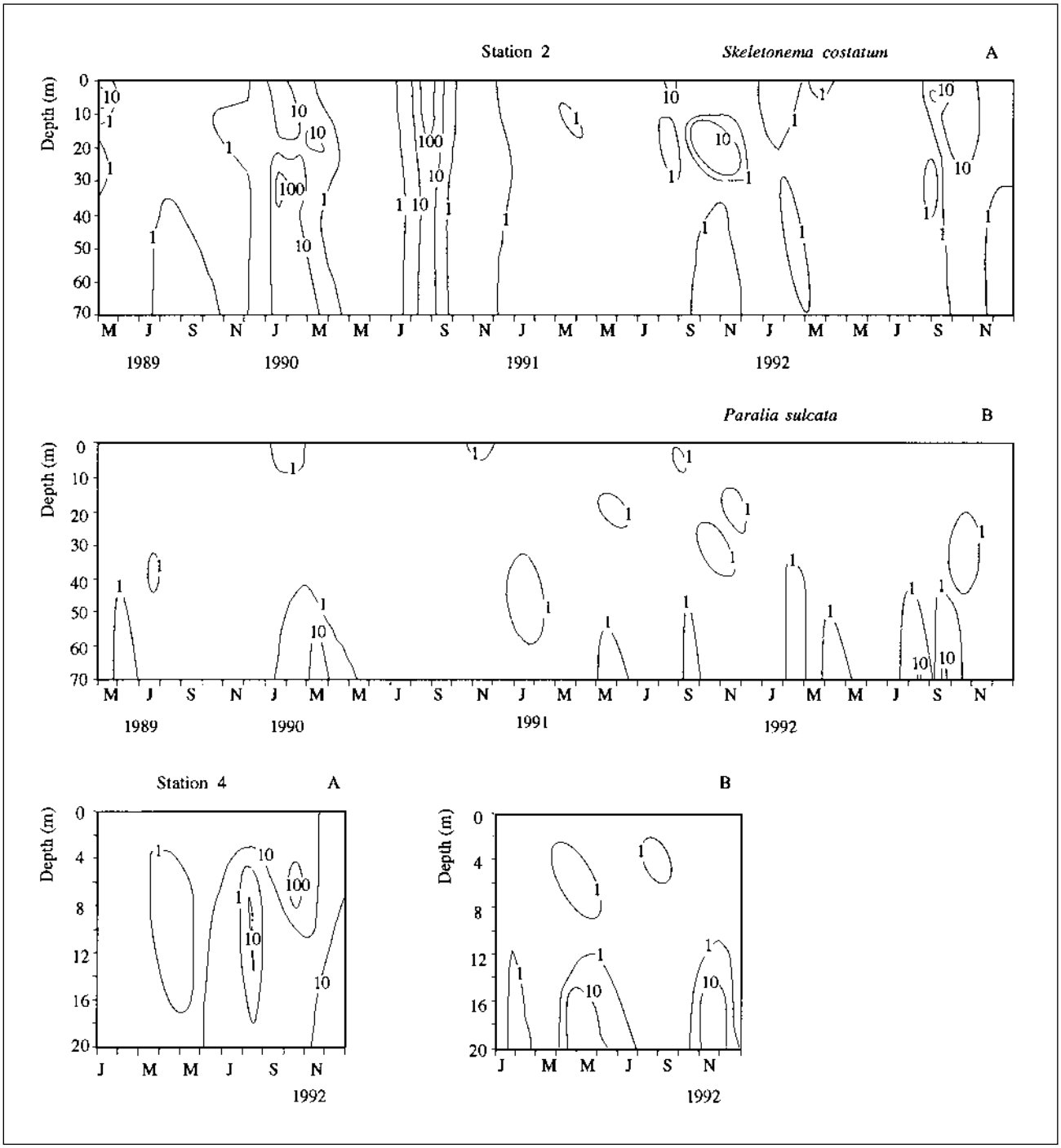


Figure 8. Distribution of abundance of some species dominant during the winter mixing period and characteristic of deeper waters: *Paralia sulcata* (A, cells ml$^{-1}$) and *Skeletonema costatum* (B, cells ml$^{-1}$)

(Fenchel, 1982), and are largely involved in the microbial loop (Azam *et al.,* 1983). In this trophic system, heterotrophic microflagellates feed on bacteria (Fenchel, 1982), and are fed by small ciliates, which in turn support micro- and mesozooplankton. It has been estimated that at the end of an upwelling event off La Coruña, this microbial system could regenerate more than 50 % of the nitrogen consumed by the phytoplankton in the area (Bode and Varela, 1994). This heterotrophic or mixotrophic component, not specifically analysed in this study, makes the identification of microflagellate trophic groups in this area a priority matter in the near future.

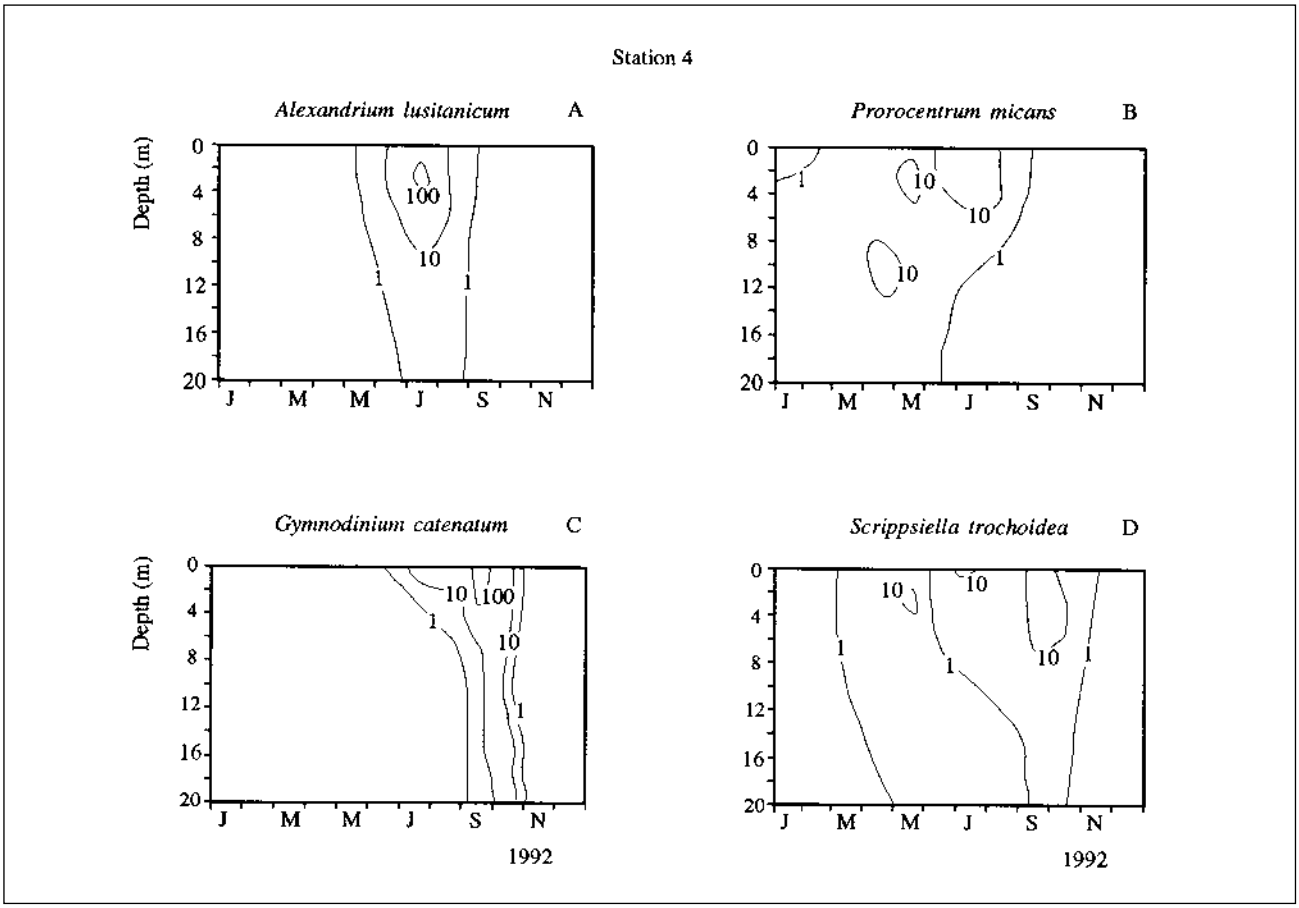


Figure 9. Distribution of abundance at station 4 of some species characteristic of periods of red tides and downwelling: *Alexandrium lusitanicum* (A, cells ml$^{-1}$), *Prorocentrum micans* (B, cells ml$^{-1}$), *Gymnodinium catenatum* (C, cells ml$^{-1}$) and *Scripsiella trochoidea* (D, cells ml$^{-1}$)

Microflagellates aside, diatoms formed the bulk of phytoplankton in the area studied, as reported previously (Valdés *et al.,* 1991). In this sense, the main characteristic of change in phytoplankton communities in the area is the developing of phytoplankton blooms in diverse situations, but generally associated with changes in surface stratification during spring and autumn, as well as during summer upwelling events. This marks a difference with respect to other coastal zones where succession is characterised by an increase in the relative dominance of dinoflagellates as conditions of thermal stratification in surface waters progress during summer (Margalef, 1978; Smayda, 1980; Harris, 1986; Fernández and Bode, 1994). A similar behaviour has been described for phytoplankton at higher latitudes, where succession does not progress up to the establishment of well defined associations of dinoflagellates, because of frequent episodes of destabilisation of the water column (Holligan, 1987). Smayda (1980) considers that succession in temperate seas starts when a change between mixing and stratification occurs and a pycnocline develops. As the day lengthens and irradiance increases, the depth of the photic zone also increases, while there is at he same time a parallel decrease in the depth of the mixed layer and as a consequence of this the spring bloom starts. The rapid growth of diatoms progresses until nutrients in the upper layer become exhausted. The spring bloom is not a continuous phenomenon, but maximum abundances appear in various pulses, with the entire process taking several weeks (Legendre, 1990). Blooms may also take place in the transition period between thermal stratification and vertical mixing caused by the first storms in autumn and/or winter. In the area studied here, the occurrence of these blooms has been related to the presence of some stratification in surface layers, and higher concentrations of chlorophyll have been associated with higher abundance of diatoms (Casas, 1995; Casas *et al.,* 1997).

Similarly, upwelling is not a continuous process either, but occurs as pulses of maximum intensity, separated by intermediate periods of upwelling-unfavourable winds (Barton, Huyer and Smith, 1977; Álvarez-Salgado *et al.,* 1993; Casas *et al.,* 1997), producing major blooms in few days. In this stage, diatoms predominate over dinoflagellates, because they are better adapted to highly turbulent environmental conditions, since they lack motility. As described for other upwelling systems, when turbulence decreases, sedimentation of diatoms out of the photic layer occurs very rapidly (Smayda and Bienfang, 1983).

This process is due not only to passive sinking, since many times downwelling drags cells at a higher speed as described by Varela *et al.* (1991) on the Galician coast.

During the phytoplankton blooms studied, *C. socialis*, *L. borealis*, *T. fallax*, *S. delicatula*, *Chaetoceros didymus* (Ehrenberg, 1845), *Navicula* spp. and *R. setigera*, were the most important species. These species are also dominant in the Rias Bajas of Galicia (Campos and González, 1975; Campos and Mariño, 1982; Varela, 1982; Campos and Mariño, 1984; Estrada, 1984; Nunes *et al.,* 1984; Figueiras and Niell, 1987a,b; Figueiras and Pazos, 1991b; Figueiras and Ríos, 1993), as well as in the Rias Altas (Blanco, 1985; Mariño *et al.,* 1985). These species lack motility, are generally colony-forming diatoms and are able to grow even faster than flagellates (Parsons, Harrison and Waters, 1978), showing low respiration rates (Laws, 1975), and large storage vacuoles (Grenny, Bella and Curl, 1973). *C. socialis* is a species of small size, able to double and even triple its biomass in 24 h (Margalef, Durán and Saiz, 1955). Likewise, *L. borealis* shows higher division rates than dinoflagellates when nutrients are not limited (Raymont, 1980). In spite of their individual small size, these diatoms form large chains, and are the main constituent of the so-called netplankton.

The presence of meroplanktonic diatoms (e.g. *P. sulcata*) and other pennate diatoms during winter due to sediment resuspension caused by very intense vertical mixing in the water column, along with small diatoms (e.g. *Skeletonema costatum*), creates an association very similar to that found in the same season in the Cantabrian Sea (Fernández and Bode, 1994) and some of the Rias Altas (Mariño *et al.,* 1985) and Rias Bajas of Galicia (Figueiras and Niell, 1987a).

A rare phenomenon, which is apart from the typical succession sequence, even though it is not infrequent in Galicia, is the red tide. Proliferations of dinoflagellates similar to those observed at station 4 in July and September 1992, have been described frequently in the Galician Rias (Margalef, 1956; Fraga, 1989; Figueiras and Pazos, 1991a,b; Jiménez *et al.,* 1992; Fraga, Bravo and Reguera, 1993; Figueiras and Ríos, 1993; Figueiras *et al.,* 1994). The main mechanism involved in the formation of red tides is the maintenance of stratified conditions in the water column, as it occurs in late summer. Dinoflagellates, because they are motile, can move through the pycnocline (which in this case is also the nutricline) and absorb nutrients from the subsurface layer. This mechanism has been described in fronts of the Bay of Biscay (Holligan, 1979) and the inner part of some Rias Bajas (Figueiras and Pazos, 1991a; Figueiras and Ríos, 1993). Even though the formation dynamic of a red tide is a very complex process, including the effect of the preferential absorption of reduced forms of nitrogen sources by some dinoflagellates (Anderson, 1989), it is known that the apparition of red tides in Galicia can be regulated by upwelling intensity (Figueiras and Ríos, 1993; Figueiras *et al.,* 1994): if upwelling is intense, diatoms are favoured, whereas when upwelling is weak, and even when it reverts to downwelling, and the nutricline sinks under the photic layer, the proliferation of dinoflagellates is favoured because they are able to utilise surface light and deep-water nutrients. In the formation of red tides, the resuspension and germination of cysts previously settled into the sediments is also important (Steidinger, 1983; Blanco, 1988). These cysts are resuspended by deep water moving through the bottom of the shelf and rising to the surface near the coast during upwelling.

In the present study, red tide episodes were found during 1992, at the inshore station, but as this station was studied only during that year, we do not know whether such episodes occurred in previous years. During recent years, red tide episodes reported for Galician coasts have noticeably increased. Fraga and Bakun (1993) consider this the result of an increasing of frequency in the pulses of upwelling-relaxation on the coast caused by the greenhouse effect, which would increase wind intensity moving towards equator. However, Lavín *et al.* (1991), have pointed out a decrease in the mean frequency of upwelling index during the 1970s,

and our data also suggest a decrease in the pulses of this index during recent years (Casas, 1995; Casas *et al.,* 1997). In any case, it is also possible that red tide generation in Galicia is closely related to the increasing eutrophication of the rias by continental runoff and urban wastewater. These discharges have high nutrient concentrations, especially organic nitrogen, and some other reduced forms of nitrogen, e.g. ammonia and urea, which could enhance dinoflagellate growth.

The data series obtained in the present study enables us to point out some interannual variations. The main variation is the decrease in the magnitude of diatom proliferations and the increase in the abundance of microflagellates and dinoflagellates. This is also a characteristic observed in long data series from the North Sea (Hickel, Mangelsdorf and Berg, 1993) and is thought to be caused essentially by increasing eutrophication in coastal areas.

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